COMPARATIVE REPRODUCTIVE BIOLOGY OF THREE SPECIES OF SWALLOWS IN A COMMON ENVIRONMENT

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ABSTRACT.—We compared the breeding biology of sympatric and contemporaneously breeding populations of Tree (*Tachycineta bicolor*), Barn (*Hirundo rustica*) and Cliff swallows (*Petrochelidon pyrrhonota*) in 1994 and 1995 in central New York to characterize their life histories under common environmental conditions. Laying dates did not vary among species, but average clutch sizes were largest in Tree Swallows (5.7 eggs), intermediate in Barn Swallows (4.7 eggs) and smallest in Cliff Swallows (3.5 eggs). Two broods were common in Barn Swallows, but Tree Swallows raised only one, and we suspect that Cliff Swallows raised only a single brood. Relative egg mass (egg mass/female mass) was higher in Barn than in Tree swallows. Most nests fledged young, and fledging success did not vary among species. Growth rates of four nestling traits were measured (mass, wing chord, tarsus and bill), and overall, Tree Swallows grew the fastest. Peak nestling mass was substantially higher in Cliff Swallows than the other species, probably because they gained the most fat. A literature survey of hirundinid growth rates also suggested that Tree Swallows grew faster than the other species. Per capita provisioning rates of parents (trips/nestling/h) increased seasonally and were highest in Barn Swallows. Slower growth despite high feeding rates suggests either lower feeding efficiency or more severe effects of ectoparasitism in Barn Swallows compared to the other species. Our results show that clutch size, number of broods/season and the pattern of nestling growth vary among species and probably represent differences that have evolved because of differences in (1) the availability of suitable nest sites (i.e., the limited breeding opportunities hypothesis), (2) food supply, or (3) demographic trade-offs. *Received 25 July 1997, accepted 11 Nov. 1997.*

Theoretical and empirical studies suggest that food supply (Lack 1968, O'Connor 1978), nest predation (Lima 1987, Martin 1995) and probability of adult survival (Saether 1988, Martin 1995) account for much of the interspecific variability that exists in reproductive traits such as clutch size, number of broods per season, and patterns of nestling growth. Much information has come from literature- or museum-based comparative studies (e.g., Ricklefs 1968, Kulesza 1990, Martin 1995), with the most revealing comparisons being of closely related and ecologically similar species that differ substantially in one or more reproductive traits (e.g., Murphy and Fleischer 1986, Martin 1988, Murphy 1989, Ricklefs 1997). A question that arises in such studies, however, is whether the presumed species level features are genetically fixed traits or represent phenotypic responses to environmental factors. Intraspecific comparisons have often shown that traits such as timing of

breeding, clutch size, egg mass and even length of incubation vary with environmental conditions (e.g., Murphy 1983, 1986; Hussell and Quinney 1987; Brawn 1991). Thus, contemporaneous studies of sympatric, related and ecologically similar species are particularly useful for characterizing reproductive patterns and identifying the ecological basis for life history differences (e.g., Turner 1982, Ekman and Askenmo 1986, Murphy 1988).

Swallows (family Hirundinidae) are a large, monophyletic group of species (Sheldon and Winkler 1993) that are all narrowly adapted to the capture of aerial insects. Many nest colonially (Shields et al. 1988) and most species nest either in abandoned cavities in trees or earthen banks, or build protected mud nests, and all temperate-zone species are migratory. Seven of the eight species that breed in North America are widely distributed (A.O.U. 1983), and despite the fact that four or five species may breed in close proximity to one another in eastern North America, Samuel (1971) published the only comparison of reproduction in sympatric populations of North American breeding hirundinids. Swallows appear to differ substantially in clutch size and possibly other traits, but given that clutch size (Hussell and Quinney 1987) and nestling growth rates (Quinney et al. 1986) of Tree

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Swallows (*Tachycineta bicolor*) vary with food abundance even over short distances, interspecific differences in clutch size and other reproductive traits of swallows in large part may be due to environmental factors and not genotypic differences. We therefore compared the breeding biology of Tree, Barn (*Hirundo rustica*) and Cliff swallow (*Petrocheldon pyrrhonota*) populations that bred in close proximity to one another to determine if previously documented differences in clutch size (Shields and Crook 1987, Robertson et al. 1992, Brown and Brown 1995) existed in sympatric populations. We also used additional information on nestling growth patterns and parental feeding rates to attempt to evaluate whether variability in swallow life histories is related primarily to characteristics of food supplies, differences in adult mortality, nest site limitation, or energetic constraints.

METHODS

Our study was conducted in 1994 and 1995 at two sites in Delaware County, NY. The main study area was located in abandoned pastures that ran along Charlotte Creek about 4.5 km east of Davenport, NY (42° 27′ N, 74° 47′ W). We established two nest box grids (15 and 16 boxes) on either side of the creek in July 1993. The grids were separated by about 100 m of stream and open field, and both were located less than 400 m from a barn that supported Barn and Cliff swallows. The second site, located 8 km away and also along Charlotte Creek, supplemented our observations from the primary site. Only Tree and Barn swallows bred at site two. We combined data from the sites because we found no differences in breeding date, clutch size, egg mass or nestling growth when comparisons were made within species.

Tree Swallow nests were visited every 2–3 days in the early breeding season to establish egg laying dates and clutch size. Breeding date was the first day of egg-laying and it was counted continuously from 1 May (e.g., 1 June = day 32). Clutch size was the number of eggs found after successive visits showed no change in the number of eggs in the nest. All eggs were marked at the blunt end with a pencil, and maximum egg length and breadth were measured with dial calipers. Unincubated eggs were weighed to the nearest 0.1 g using a 10 g Pesola scale. Fresh egg mass was estimated for other eggs using length and breadth measurements (e.g., Murphy 1983). We made daily visits around the expected hatching date to determine hatching success and initial brood size, and then visited nests every 2–3 days during the nestling period to measure changes in nestling mass (0.1 g using either a 10 or 50 g Pesola scale), and growth of the tarsometatarsus (=tarsus), bill (anterior edge of nares to bill tip) and wing chord [all linear measurements made to

the nearest 0.05 mm using dial calipers with the exception of wind chord (nearest 0.5 mm with wing ruler)]. We followed the same procedures with Barn and Cliff swallows, but because they nested at less accessible locations (mainly Cliff Swallows) we obtained fewer data and more time elapsed between nest checks (2–5 days). We often had to remove a portion of the neck of the gourd-shaped mud nest of the Cliff Swallow to gain access. Parents repaired the damage, but for this reason also we visited their nests less frequently. Most Barn Swallow nests were located on the tops of beams inside the two barns. Cliff Swallows attached their nests directly to the outside wall of the barn. To prevent the accidental loss of Cliff Swallow nests when we removed eggs and/or nestlings, in 1995 we reinforced many of the nests by stapling a sheet of fiberglas screening over the nest to the eaves of the barn.

In lieu of measuring food supply, in 1995 we made one hour observations of the rate of parental feeding visits to nests to measure foraging efficiency. All three species feed their young a bolus of small insects that have been captured from the air, and in making the comparison of feeding rate we assume that all parents attempted to feed their young with equal vigor and that one nestling was fed per visit (Turner 1982, Brown and Brown 1995). A small hill that overlooked the Tree Swallow colony allowed simultaneous observations of several nests. We could also observe Tree and Barn swallow nests simultaneously at site 2. In all cases, we made observations between 08:00 and 12:00 EST (none during poor weather).

We used the STATISTIX (version 4.1, Siegel 1992) and the general linear models procedure of SAS (SAS 1992) to test for annual and interspecific differences in reproduction and nestling growth. Standard parametric statistics (analysis of variance, *t*-tests, least squares linear regression) were used to compare breeding date, clutch and egg size among species and years. Equivalent nonparametric statistics were used when variances were heteroscedastic. Nestling growth rates were computed using least squares linear regression during the period of linear growth. This corresponded to days 3–10 (hatching = 1) for mass, day 5 onward for wing chord, days 1–10 for tarsus and days 3–14 for bill. Each nest was treated as a single observation; hence, the statistics (mean, SD, *n*) given below always reflect the number of nests from which data were collected. We also described changes in nestling mass with age by calculating growth rates using Ricklefs' (1967) graphical method. Unless otherwise stated, statistical significance was established at $P \leq 0.05$. All statistical analyses were performed with SAS (ver. 6.12) on a DEC Alpha 2100A/250 under OpenVMS.

RESULTS

Breeding statistics.—Tree Swallows initiated clutches significantly earlier in 1995 than in 1994 ($t = 5.62$, $P < 0.001$), and although Barn Swallows showed the same trend, annual

TABLE 1. Reproductive statistics for sympatric populations of Tree, Barn and Cliff swallows breeding in Delaware Co., NY, during the 1994 and 1995 breeding seasons.

Species	Year	Laying date[a] $\bar{x}$ (SD; n)	Clutch size $\bar{x}$ (SD; n)	Egg mass (g) $\bar{x}$ (SD; n)
Tree Swallow	1994	25.0 (6.60; 14)	5.8 (0.70; 14)	1.85 (0.158; 14)
	1995	14.2 (3.63; 24)	5.7 (0.74; 25)	1.85 (0.141; 23)
Barn Swallow	1994	26.6 (11.07; 11)	4.5 (0.97; 13)	1.90 (0.128; 9)
	1995	19.4 (8.44; 10)	5.1 (0.57; 10)	1.86 (0.130; 8)
Cliff Swallow	1994	31.0 (6.20; 5)	3.3 (1.21; 6)	2.19 (0.097; 5)
	1995[b]	65.2 (3.06; 6)	3.7 (1.03; 6)	2.15 (0.147; 6)
Two-way ANOVA		F (*P*)	F (*P*)	F (*P*)
Species		1.58 (>0.05)	40.76 (<0.001)	24.06 (<0.001)
Year		12.36 (0.001)	0.12 (>0.05)	0.14 (>0.05)
Species × year		0.47 (>0.05)	0.31 (>0.05)	0.22 (>0.05)

[a] Dates counted consecutively with day 1 = 1 May.
[b] 1995 Cliff Swallow statistics refer to late breeding attempts.

differences were not significant (Table 1; $t = 1.67$, $P > 0.05$). Cliff Swallows laid eggs during the period of first clutches in 1994, but did not lay again at our site until Barn Swallows initiated second clutches in 1995 (Table 1). Results of a two-way analysis of variance (ANOVA) with year and species as main effects indicated that only the effect of year was significant (Table 1). Tree Swallows raised one and most Barn Swallows raised two broods. Second clutches of Barn Swallows were laid an average of 39 days after the start of first clutches in 1995, and at the same time as Cliff Swallows ($t = 1.09$, df = 11, $P > 0.05$). In both years Cliff Swallows appeared to raise only a single brood.
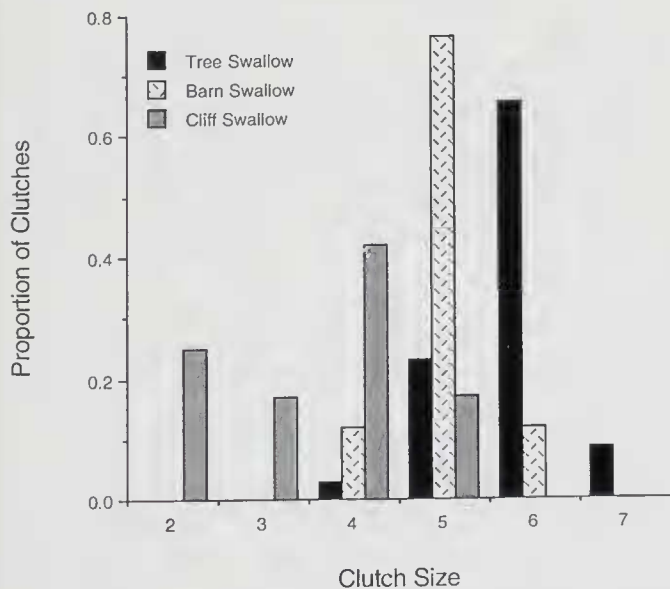

FIG. 1. Comparison of clutch sizes of Tree, Barn and Cliff swallows breeding in Delaware County, NY, in 1994 and 1995.

Modal clutch size of Tree Swallows was six eggs ($\bar{x} = 5.7$, SD = 0.72, $n = 39$). Barn Swallows usually laid five eggs in first clutches ($\bar{x} = 4.7$, SD = 0.86, $n = 23$), while 3–4 eggs were typical of Cliff Swallows ($\bar{x} = 3.5$, SD = 1.09, $n = 12$; Fig. 1). A two-way ANOVA (species and year) showed that the species effect was significant, but that year and species × year interaction were not (Table 1). Clutch size declined with date when all three species were combined ($r = 0.405$, df = 55, $P < 0.002$). Slight differences in date might have contributed to the clutch size differences, but after removing date effects the species differences persisted ($F = 13.64$, df = 2, 54, $P < 0.001$). Residual clutch size was 0.6 and 1.6 eggs larger in Tree Swallows than Barn and Cliff swallows, respectively (Tukey's test: $P < 0.05$). Barn Swallows laid more eggs in first than in second nests ($\bar{x} = 4.0$, SD = 0.19, $n = 8$; $t = 2.26$, $P = 0.03$).

Egg mass did not differ among years but Tree and Barn swallows produced significantly smaller eggs than Cliff Swallows (Table 1). Cliff Swallows (23.4 g; Brown and Brown 1995) are heavier than Barn (19.6 g; R. Montgomery, pers. comm.) and Tree swallows (21.1 g; Robertson et al. 1992), which possibly explains the larger Cliff Swallow eggs. We thus compared relative egg mass [arcsine(egg mass/adult mass)] and found that Barn Swallows laid relatively larger eggs (0.097) than Tree Swallows (0.088), but Cliff Swallows (0.093) did not differ from either species ($F = 16.62$, df = 2, 69, $P < 0.001$; *a posteriori* comparisons made using Tukey's test).
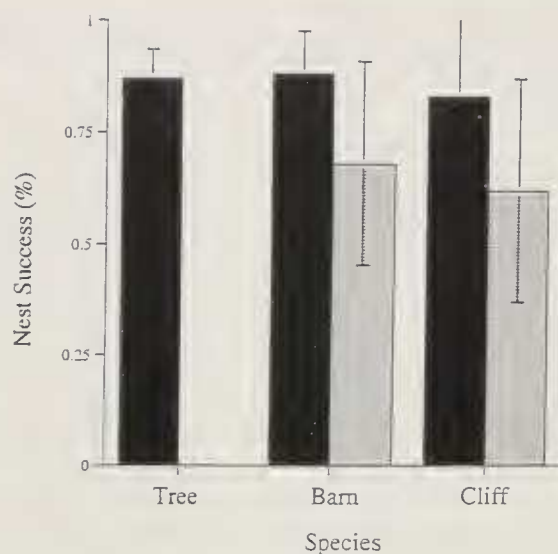
FIG. 2. Fledging success (nestlings fledged/egg laid) for Tree, Barn and Cliff swallows breeding during 1994 and 1995 in Delaware Co., NY. Black bars refer to early (or first) nests of the season and shaded bars represent late (or second) nests. The vertical lines indicate ±2 standard errors.

No nests were lost to predation, and most losses resulted from the starvation of 1 or 2 nestlings within a nest. Regardless of species, about 85% of young fledged from broods that were raised during June (Fig. 2; $F = 0.11$, df $= 2, 54$, $P > 0.05$). Second broods of Barn Swallows and the late 1995 Cliff Swallow nests tended towards lower success than that of the early broods (Fig. 2), but the difference was not significant in either Barn ($t = 1.95$, df $= 22$, $P > 0.05$) or Cliff swallows ($t = 1.39$, df $= 9$, $P > 0.05$).

Nestling growth.—The rate at which nestlings gained mass did not differ between years in Tree ($t = 0.96$, df $= 18$ broods, $P > 0.05$), Barn ($t = 1.44$, df $= 21$, $P > 0.05$) or Cliff swallows ($t = 0.12$, df $= 9$, $P > 0.05$). Likewise, first and second broods of Barn Swallows grew at virtually identical rates in 1995

($t = 0.63$, df $= 15$, $P > 0.05$). Analysis of wing chord growth yielded identical results. Slight annual differences were found for tarsus and bill growth of Tree Swallows, but because the differences were small compared to interspecific variation, we combined all data between years before comparing species.

Growth rates of all four traits differed significantly among species (Table 2). Cliff Swallows gained mass 13% faster than Barn Swallows, and although Tree Swallows were closer to Cliff Swallows, their growth rate did not differ from either species (Tukey's test: $P > 0.05$). The peak mass of Cliff Swallows was 21% and 31% higher than that of Tree and Barn swallows, respectively (Fig. 3, Table 2), and the 8% higher peak mass of Tree Swallows compared to Barn Swallows was also significant (Tukey test: $P < 0.05$). Differences in the rate of wing chord growth were not large, but the wing chords of Tree Swallows grew faster than those of Cliff Swallows (Table 2). On the other hand, the tarsae of Cliff Swallows grew the fastest and Barn Swallows the slowest (Table 2). Tree Swallows did not differ from either species. Finally, growth of the bill was slower in Cliff than in both Barn and Tree swallows (Table 2).

Feeding rates.—Per capita provisioning rates to first broods of Tree and Barn swallows increased with nestling age ($r = 0.543$) and date (late May through mid June; $r = 0.674$, df $= 39$, $P < 0.001$ for both). We therefore included both variables and both species in a multiple regression analysis of per capita feeding rate. All three variables contributed significantly to the model (t-test on type III sums of squares: date, $P < 0.001$; nestling age, $P = 0.001$; species, $P < 0.001$; model R^2 $= 0.783$, df $= 3, 37$, $P < 0.001$). After con-

TABLE 2. Summary statistics describing nestling growth rates for Tree, Barn and Cliff swallows breeding in Delaware Co., NY, during the 1994 and 1995 breeding seasons. Species sharing the same letter do not differ significantly from one another (n = number of nests).

Variable	Tree Swallow $\bar{x}$ (SD; n)	Barn Swallow $\bar{x}$ (SD; n)	Cliff Swallow $\bar{x}$ (SD; n)	Statistic F or H (P)[a]
Mass gain (g/d)	2.14 (0.29; 20)AB	1.96 (0.29; 23)B	2.21 (0.32; 11)A	3.45 (0.039)
Peak mass (g)	23.3 (1.22; 32)B	21.6 (1.47; 20)C	28.3 (1.84; 11)A	80.03 (<0.001)
Wing growth (mm/d)	5.49 (0.20, 19)A	5.35 (0.44; 22)AB	5.15 (0.44; 12)B	6.06 (0.048)
Tarsus growth (mm/d)	0.96 (0.10; 22)AB	0.84 (0.16; 21)B	1.08 (0.38; 8)A	9.97 (0.007)
Bill growth (mm/d)	0.25 (0.04; 20)A	0.25 (0.04; 23)A	0.21 (0.04; 11)B	4.13 (0.02)

[a] F and H refer to results of analysis of variance and Kruskal-Wallis tests, respectively.
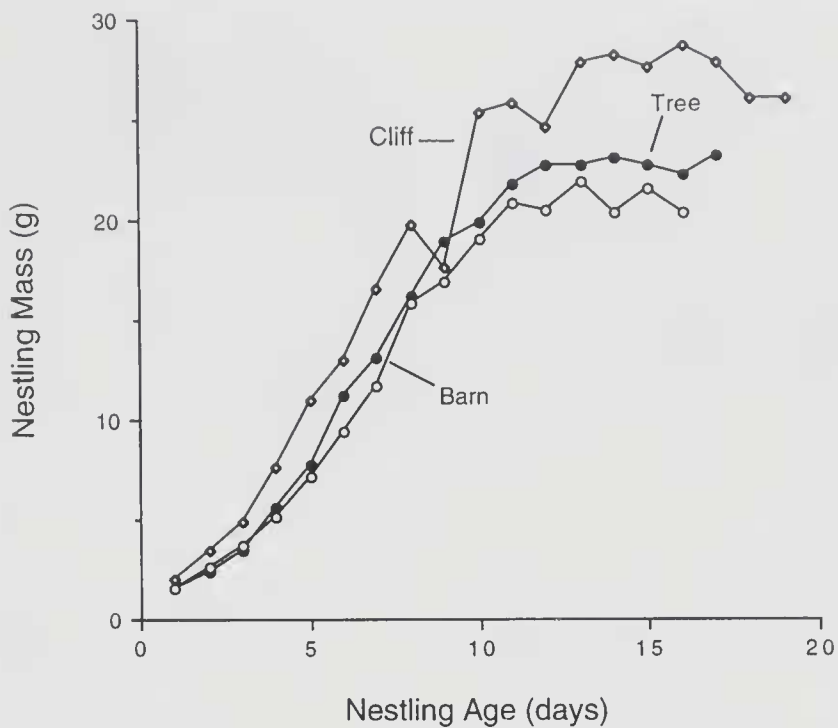
FIG. 3.   Increase in mass of nestling Tree (●), Barn (○) and Cliff swallows (◊) from populations that bred sympatrically in Delaware Co., NY, in 1994 and 1995.

trolling for the effects of date and age, residual feeding rate of Barn Swallows ($\bar{x}$ = 0.9 trips/nestling, SD = 2.00, n = 14) was higher than that of Tree Swallows ($\bar{x}$ = −0.5, SD = 0.99, n = 27; $t_{\text{unequal variance}}$ = 2.46, P = 0.025). Per capita feeding rates to late Barn and Cliff swallow broods varied with brood size (r = −0.664, df = 19, P = 0.001). After removing the effect of brood size, Barn Swallow residual feeding rate ($\bar{x}$ = 0.7 trips/nestling, SD = 1.19, n = 11) was slightly but not significantly higher than that of Cliff Swallows (−0.8, SD = 3.58, n = 10; $t_{\text{unequal variance}}$ = 1.24, P > 0.05). Residual per capita feeding rate to first (−0.1 trips, SD = 2.66) and second (0.2 trips, SD = 1.66) Barn Swallow broods did not differ (t = 0.35, P > 0.05) after accounting for the negative correlation of per capita feeding rate with brood size.

DISCUSSION

Our description of interspecific differences in clutch size and number of broods per season are consistent with previously published reports in showing that Tree Swallows lay the largest clutches and produce only a single brood per year (Robertson et al. 1992). The Barn and Cliff swallows also differed significantly in clutch size (Samuel 1971, Grant and Quay 1977, Shields and Crook 1987, Brown

and Brown 1996, this study) and in number of broods per season (often 2 in *H. rustica*, and 1 in *P. pyrrhonota*; Shields and Crook 1987, Brown and Brown 1995). On the other hand, when all three species were present neither breeding date nor fledging success differed among them. The larger Tree Swallow clutches in part might be related to the use of nest boxes with a large internal space (Robertson and Rendell 1990), but we doubt that this is the principal explanation for the interspecific differences since in our population we have found no relationship between clutch size and cavity floor area despite large variation in the latter variable (M. T. Murphy, unpubl. data). Goodman (1982) also reported that clutch size was independent of nest cup volume in Barn Swallows. Given the similarity in timing of breeding, proximity to one another, and exposure to identical climatic conditions, the interspecific differences in clutch size and number of broods most likely represent evolved differences rather than proximate responses to weather or food supply (e.g., Hussell and Quinney 1987).

Although less dramatic, rates and patterns of nestling growth also differed. Based on absolute growth rate (Table 2), nestling Tree Swallows grew either the fastest (wing chord) or equalled the most rapidly growing species
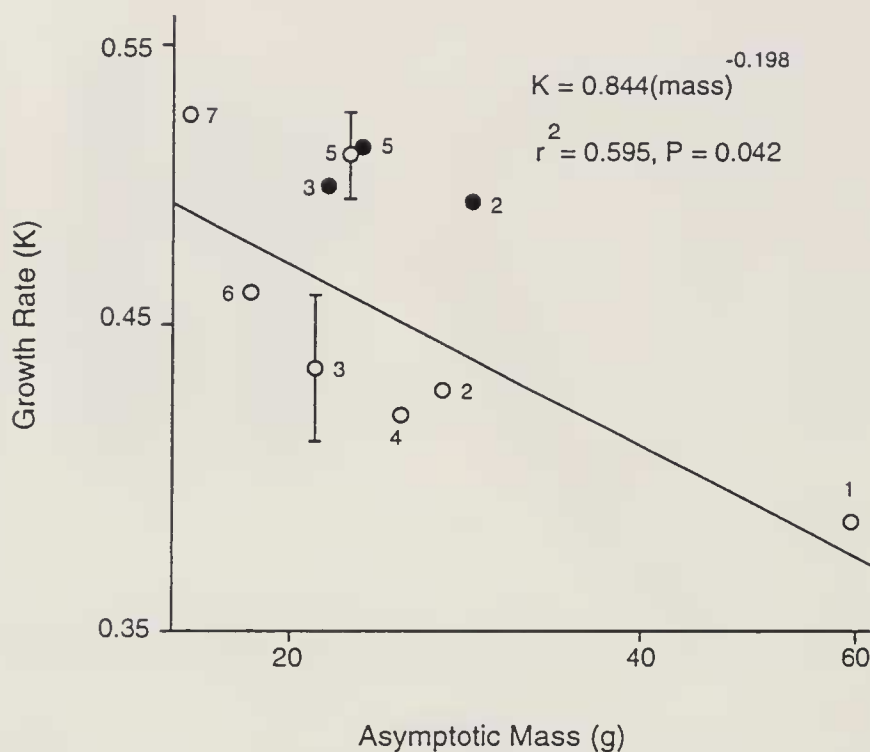
FIG. 4. The relationship between nestling growth rate (K of Ricklefs 1967) and asymptotic mass for swallows breeding in north temperate latitudes. Open circles represent literature data (see Appendix). Filled circles are for the Tree, Barn and Cliff swallow populations in this study. Numbers refer to species: 1 = *Progne subis*; 2 = *Petrochelidon pyrrhonota*; 3 = *Hirundo rustica*; 4 = *Delichon urbica*; 5 = *Tachycineta bicolor*; 6 = *Stelgidopteryx serripennis*; 7 = R*iparia riparia*. Vertical bars for *H. rustica* and *T. bicolor* are ±2 standard errors around the mean (*n* = 3 and 4, respectively), and do not include data reported here. Likewise, the power equation relating growth rate to mass does not include our data, but is based on the mean for the seven species shown [*T. thalassina* was not included (see Appendix) because growth data were derived from a single brood].

for mass, tarsus and bill. Mass and tarsus growth were slower in Barn Swallow nestlings than the other species, and Cliff Swallow nestlings exhibited the slowest wing chord and bill growth rates. Nestlings of all three species exceeded adult mass (as is typical of hirundinids), but Cliff Swallows in particular were very heavy compared to the other species. Cliff Swallows remain in the nest for about 24 days (Samuel 1971, Brown and Brown 1995), Barn Swallows usually fledge at 21 days (Shields and Crook 1987), but Tree Swallows take only 18–22 days (Robertson et al. 1992). The shorter nestling period of Tree Swallows follows from their rapid growth, while the long nestling period of Cliff Swallows is probably related to their slow wing growth and relatively large mass.

Differences in adult size confound comparisons of growth rate because growth rate and size tend to be negatively related (Ricklefs 1968). To provide a basis for evaluating our results, we compared growth rate (K; Ricklefs 1967) for our three populations, and for other populations and species of temperate-zone breeding swallows (Appendix). Our estimate of Tree Swallow growth rate (K = 0.510) was slightly faster than sympatric Barn (K = 0.496) and Cliff swallows (K = 0.490). Among the sample of seven species of temperate zone breeding swallows with data, growth rate declined significantly with asymptotic nestling mass (Fig. 4). We used this relationship to predict expected growth rates for all populations (based on asymptotic mass). Comparisons of residual growth rates (observed rate − predicted rate) showed that Tree Swallows (0.04, SD = 0.014, *n* = 5 studies) grew faster ($t_{unequal\ variances}$ = 3.31, *P* = 0.03) than Barn Swallows (−0.02, SD = 0.035, *n* = 4 studies) when the effect of body size was removed. Clearly, it is impossible to fully characterize nestling growth in any species without examining spatial and temporal variability, but given the available data, we conclude that Tree Swallows grow relatively rapidly and that Cliff Swallows gain relatively more mass (probably fat) prior to fledging than other swallows.

Interspecific differences in clutch size.—We

are unaware of any attempts to explain why the life histories of these species differ to such a degree. Taxonomic affiliation seems unlikely since differences in clutch size can be large even among congeners [e.g., clutch sizes of Violet-green (*T. thalassina*) and Tree swallow differ significantly; Brown et al. 1992 and Robertson et al. 1992], and other traits, such as coloniality, are not constrained by phylogeny (Shields et al. 1988). Nest predation has probably not been a major force shaping their differences because so few nests are lost to predators (Shields et al. 1988). Moreover, trends within swallows are opposite of the theoretical predictions. Large clutch size is generally associated with low nest predation rates (Martin 1995), yet Tree Swallows lay the largest clutches and under natural conditions probably lose more nests to predators than either of the other species (Shields et al. 1988, Rendell and Robertson 1989). We suggest the following as plausible explanations for the differences in clutch size, and possibly other traits: (1) foraging behavior and food supply; (2) demographic adjustments to adult mortality; (3) energetic costs of nest construction; and (4) nest site limitation.

Although these species are highly adapted to aerial insectivory, and thus susceptible to sudden and sometimes drastic declines in food supplies as a result of poor weather (Bryant 1973, Turner 1982, Brown and Brown 1995), their foraging behaviors differ. Cliff Swallows tend to forage at heights of 50 m or more above ground (Brown and Brown 1995) but Barn and Tree swallows generally forage much lower, often just above the surface of fields and streams (Samuel 1971, pers. observ.). Variability in aerial insect abundance increases with altitude (Lack 1968, Bryant 1973), and Brown (1986) has shown that Cliff Swallows exhibit behaviors indicating that they use highly variable food supplies. Albeit limited, our observations indicate that Cliff Swallows had the most variable feeding rates. Theory predicts a reduction in clutch size when food supplies vary unpredictably and to the point that the risk of failure caused by the complete starvation of large broods is high (Murphy 1968). Thus, the small clutches of Cliff Swallows may represent an adaptation to the use of highly variable food supplies. The high provisioning rates of Barn Swallow (but

which did not support higher growth rates) also suggests that Tree and Barn swallows either forage in different strata or habitats, or that they capture different prey (e.g., Turner 1982).

Demographic trade-offs between reproduction and adult survival can be driven by either extrinsic mortality (e.g., storms, predators) or costs of reproduction (Williams 1966, Charnov and Krebs 1974), but in either case high adult mortality favors early breeding and high fecundity (Law 1979, Reznick et al. 1990, Stearns 1992). There is little to no evidence for the existence of reproductive trade-offs in swallows (DeSteven 1980, Bryant 1979, Wheelwright et al. 1991), but annual survivorship does appear to differ among these species, possibly from events in the nonbreeding season. Brown and Brown (1995) used Jolly-Seber stochastic models to show that 57% of Cliff Swallow adults survived between breeding seasons. Barn and Tree swallow survivorship has not been estimated with the same methods, but survivorship estimates based on Farner's (1955) approach are higher for Cliff Swallows (48%) than for both Barn (42%) and Tree (40%) swallows (data from Martin 1995). The small clutch size of Cliff Swallows is thus consistent with their relatively higher survivorship.

Tree Swallows differ from the other species in that they nest in abandoned tree cavities, and individuals failing to secure a cavity do not breed. Although Barn and Cliff swallows build their own nests, and most birds probably secure a mate and breed, natural sites suitable for the placement of Barn Swallow nests may be limited (Speich et al. 1985). On the other hand, Brown and Brown (1995) stated that there was no evidence for a shortage of either colony or nest sites for Cliff Swallows. The nest site limitation hypothesis predicts that females should invest heavily in reproduction when breeding opportunities are limited (Martin 1993, Beissinger 1996), and in accordance, clutch sizes of these three species are directly correlated with nest site shortage. Moreover, other predictions (see Beissinger 1996) of the limited breeding opportunities hypothesis lend qualitative support. Intraspecific nest takeover and infanticide occur among Tree Swallows (Robertson 1990), and Tree Swallows lose nests to larger secondary cavity nesters (Rob-

ertson and Rendell 1990). Shields and Crook (1987) found evidence of infanticide in Barn Swallows and attributed it to competition for limited nesting sites. Additional predictions of the limited breeding opportunities hypothesis for which data are lacking are that the proportion of nonbreeding individuals and average age of first reproduction should be highest in Tree Swallows (see Beissinger 1996).

The energetic costs of nest construction probably also vary among swallows in a way that could account for the differences in clutch size. Nest building in Tree Swallows entails only the collection of twigs and feathers to line their cavity nest. Barn and Cliff swallows, on the other hand, carry considerable amounts of mud to build a complicated nest. Shields and coworkers (1988) estimated that a new Barn Swallow nest required between 1000 and 2000 mud gathering trips. Cliff Swallow nests are larger; they are attached directly to the vertical face of a surface, and probably require even more mud gathering trips than Barn Swallows. A trade-off may exist between clutch size and the energetic cost of nest construction. In fact, Brown and Brown (1996) reported that clutch size declined significantly with increasing nest size in Cliff Swallows. On the other hand, Barn Swallows that reused nests (and therefore avoided the heavy cost of nest construction) had the same seasonal egg production as females with new nests (Shields et al. 1988).

At present we cannot unequivocally exclude any of the hypotheses that we have proposed to explain the differences in clutch size and annual fecundity of Tree, Barn and Cliff swallows. Considerable evidence supports the nest site limitation hypothesis. In addition, the apparent differences in annual survival that are consistent with the demographic trade-off hypothesis might arise from selection for higher reproductive effort by the nest site limited species. However, differences in nestling growth exist that are also consistent with the food supply hypotheses. For instance, Tree Swallows grew faster than Barn Swallows despite lower feeding rates. Tree Swallows thus appear capable of providing more food per unit effort than Barn Swallows, which may indicate that they exploit a more abundant and/or more stable food supply. Two other explanations for the seemingly more efficient

growth of Tree Swallows are that (1) they experience less severe ectoparasite infestations than the other species (Shields and Crook 1987, Brown 1988), and (2) poor nestling Barn Swallow growth might stem from a poorly insulated nest. Barn Swallow nests are very open and exposed compared to the cavity nests of Tree Swallows, and nestling Barn Swallows may use more energy thermoregulating than do nestling Tree Swallows.

Differences in peak nestling mass also suggest that food supplies differ among these species. Nestling birds use fat as insurance against temporary food shortages (Lack 1968, Bryant and Hails 1983), and nestling fat content and variability in insect abundance increase with average adult foraging height in aerial insectivores (Bryant and Hails 1983). Cliff Swallows forage higher than the other species, lay the smallest clutches, have the most variable feeding rates, their nestlings grow relatively slowly (yet attain the greatest peak mass) and remain in the nest longer than Tree and Barn Swallows. These patterns all suggest that Cliff Swallows experience high stochastic variation in food supplies. Barn Swallows are perhaps the most perplexing in that nestling growth is not rapid, despite the fact that they alone regularly raise two broods. Perhaps historical differences in geographic distribution and length of the breeding season (more southern and longer in the Barn Swallow) favored multiple broods that grow at moderate rates. Without the option of second broods and potential intraseasonal costs of reproduction (McGillivray 1983, Smith et al. 1987), larger clutches and rapid growth would have been more likely to evolve in Tree Swallows.

We do not purport to have explained why clutch size, number of broods and growth rates differ among these species. However, our data strongly point to the need to test additional predictions of the limited breeding opportunities (Beissigner 1996) and measure for differences in the abundance and variability of food supplies. In addition, comparative studies of survivorship in sympatric populations of three or more swallows in which rigorous statistical models (Nichols et al. 1994) are used to estimate survival would be highly instructive for testing the negative relationship that may exist between fecundity and survival in these and possibly other passerines (Martin 1995).

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APPENDIX. Comparative nestling growth statistics for North American and European populations of hirundinids. K and t_{10-90} were calculated using Ricklefs (1967) graphical method. R is the ratio of asymptotic nestling mass to adult mass.

Species	Mass (g) Adult	Mass (g) Asymptote	K	t_{10-90}[a] (days)	R	Location	Source[b]
Progne subis	50.2	60.0	0.385	11.40	1.20	Kansas	1
Hirundo rustica	17.8	20.5	0.453	9.70	1.15	New York	1
	19.6	21.6	0.432	10.20	1.10	New York	2[c]
	19.6	20.7	0.412	10.80	1.06	New York	2[d]
	19.6	21.5	0.496	8.85	1.10	New York	3
Hirundo pyrrhonota	20.1	27.0	0.426	10.30	1.34	New York	1
	23.4	28.5	0.490	9.00	1.22	New York	3
Delichon urbica	19.4	24.8	0.418	10.50	1.28	England	4
Tachycineta bicolor	21.1	22.0	0.488	9.00	1.04	New Brunswick	1
	20.1	22.6	0.502	8.74	1.12	Manitoba	5
	21.6	23.8	0.526	8.35	1.10	Ontario	6[e]
	21.6	21.5	0.514	8.54	1.00	Ontario	6[f]
	21.6	23.0	0.510	8.61	1.09	New York	3
Tachycineta thalassina	14.8	21.5	0.410	10.70	1.45	Washington	1
Stelgidopteryx serripennis	15.6	18.5	0.458	9.60	1.18	Michigan	1
Riparia riparia	13.7	16.4	0.523	8.40	1.20	England	7

[a] Indicates the time required to complete between 10% and 90% of asymptotic mass.
[b] Code to references: 1 = Ricklefs 1968; 2 = Shields and Crook 1987 ([c] and [d] refer to parasite-free and parasitized young); 3 = this study; 4 = O'Connor 1978; 5 = Zach and Mayoh 1982; 6 = Quinney et al. 1986 ([e] and [f] refer to high food and low food environments); 7 = Turner and Bryant 1979.